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THE EFFICIENCY OF FOUR SELECTION
SCHEMES FOR IMPROVEMENT
OF COLD TOLERANCE AND
DISEASE RESISTANCE IN MAIZE

BY

ANDREW ROCHOLL BETTENDORF

A thesis submitted
in partial fulfillment of the requirements for the
degree Master of Science
Major in Plant Science

South Dakota State University
1984

THE EFFICIENCY OF FOUR SELECTION
SCHEMES FOR IMPROVEMENT
OF COLD TOLERANCE AND
DISEASE RESISTANCE IN MAIZE

This thesis is approved as a creditable and independent investigation by a candidate for the degree, Master of Science, and is acceptable for meeting the thesis requirements for this degree. Acceptance of this thesis does not imply that the conclusions reached by the candidate are necessarily the conclusions of the major department.

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DEDICATION

My thesis is dedicated to my loving wife, Anne, for her support and encouragement throughout my graduate study.

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INTRODUCTION

The economic worth of any individual (plant or animal) is usually dependent on more than one trait. Since there is usually more than one trait involved in selection, a breeders problem is determining the relative importance of each of these traits. They must then be placed in some logical order so that the best material is selected for the following generations. Arriving at reasonable economic weights for each trait may be fairly difficult, especially if not much is known about the material one is working with. Other factors to consider when selecting within a population are, how heritable the trait is and is it independent of other, less desirable traits. The most efficient selection scheme used is determined by the largest genetic gain per unit of time and effort expended (28).

The objective of this study was to determine the relative efficiency of four selection schemes for simultaneous improvement of six uncorrelated traits in maize. Three modified selection indices (20,69,72) were evaluated along with the independent culling method of selection (28). The traits chosen for improvement by one cycle of recurrent selection were: 1) emergence index, 2) percent emergence, 3) seedling dry weight, 4) resistance to Northern Corn Leaf Blight 5) resistance to Goss' Wilt and 6) resistance to Diplodia stalk rot.

LITERATURE REVIEW

Selection Schemes

The goal of many plant breeders is to be able to efficiently select improved material for more than one trait at a time. There are two main methods for simultaneous character selection available; the index selection method, first proposed by Smith (83) and independent culling levels (28). The former selection method, taken in a broad sense, has been used by breeders for many years. However, independent culling levels has not often been used by maize breeders on a formal basis (26).

The two selection methods used are considered fairly efficient methods by plant and animal breeders (21,28,100,101). The relative efficiency of a selection method is determined by that which gives the maximum genetic improvement per unit of time and effort expended (28). Index selection or "total score method" described by Hazel and Lush (28) can be used to select for all traits simultaneously. This is accomplished by employing an index of net merit constructed by adding into one figure the credits and penalties given each unit of selection according to the degree of its superiority or inferiority for each trait.

Independent culling levels has had limited use and success when used in a breeding program (14,77). Independent culling

levels is defined as a system where a certain level of merit is established for each trait, and all individuals outside that level are discarded, regardless of their rank within other traits (28).

There are a number of factors influencing relative efficiencies of selection schemes including: selection intensity, heritabilities, the number of traits under selection, their relative importance, (which is based on economic weight), and correlations between them (100). Hazel and Lush (28) compared the efficiencies of these methods in terms of genetic gain for uncorrelated traits with equal variances and heritabilities. They concluded that the index method was more efficient than the independent culling levels method. According to Young (100), when dealing with two negatively correlated traits of equal importance, the index method is best when selection pressure is low, but if selection intensity is high, then independent culling levels may be more appropriate because of the relative simplicity of operation. Young (100) also points out that the superiority of an index over other methods increases with an increasing number of traits under selection, but decreases with increasing difference in relative importance. That is, it is highly efficient when the traits being considered are equally important. Smith et al. (85) stated that even though the number of traits that can be included in the index is unlimited, the more traits that are in the index, the smaller the gain will be for each individual trait.

Whatever index is used, an index cannot determine the relative importance of each trait (85). Justification for putting some weights or desired levels of selection for each trait is that it forces the breeder to set up criteria for what the desirable characteristics are and their relative importance. Part of the criticism of an index is that inaccurate estimates can be made for genotypic variances so that some characteristics appear to be more or less heritable than they actually are (28). One may also fail to consider properly the effects of genetic and environmental correlations between traits (26).

The independent culling levels may be seriously criticized for the fact that independent culling levels are not determined statistically and genetic advances are not optimized (77). In using independent culling levels, care must be taken not to set levels too severe for one trait and too low for another. It has been shown that at a given level of selection, increasing the selection level on one trait automatically reduces pressure that may be applied to other traits (28). For correlated traits, the theory of optimum, independent culling levels has not been developed beyond two-trait selection (101). Rosielle and Frey (77) stated that independent culling levels was preferably used by plant breeders when selection is used in early generation for highly heritable traits, such as heading date and height, followed by extensive testing and selection for less heritable traits, such as grain yield.

There are several variations of Smith's (83) original selection index in use today. Some of these indices require estimates of heritabilities, of variances and covariances values (28), relative economic weights as index weights (97) or desired gains used for index weights (72). These methods are thought to be fairly efficient when valid estimates of the desired parameters are available (26,97). There are other cases where breeders do not have accurate estimates of genetic variance and heritabilities so that accurate weights cannot be applied (7). Some researchers feel that weight free (relative weighting) or parameter free (do not use genetic variance or covariance) indices would be more useful and accurate in these situations (20,69).

Each type of index may have its value for a particular set of circumstances. The index described by Pesek and Baker (72) uses "desired gain" values instead of economic weights for a group of quantitative traits. The main requirements in using a desired gain index are quantitative data, estimates of genetic parameters and a statement of the goals of the program. This method combines the goals of the breeder and the genetic restrictions of the population in which they are working into an objective scale for selection.

Suwanaradon et al. (88) found that when desired gains were used with S_1 recurrent selection, 14 cycles or 28 years of selection would be needed to reach the predicted values for seven

traits. This method was estimated to give only half the improvement for yield compared to selection for yield alone. Mock and Eberhart (64) tested two adapted maize populations (BSSS13 and BSSS2) and found there was a significant increase in the cold tolerance traits (percent emergence, emergence index, and seedling dry weight) when using predicted gains in S_1 recurrent selection programs. Mock and Bakri (63) reported greater relative progress for improvement in cold tolerance traits in BSSS13 than in BSSS2 when using desired gains in the selection index. They felt the lack of improvement in the BSSS2 population was due mainly to the lower amount of variability found in the population. Kauffmann and Dudley (49) found that with the desired gain index (DGI) it is possible to simultaneously improve negatively correlated traits such as yield and percent protein.

Crosbie et al. (7) found DGI to be very poor when relatively large gains were specified for one trait and small gains desired for another. They also found it difficult to specify meaningful desired gains for emergence index and seedling dry weight. It is important that desired gains for minor traits not be set too high, because doing so reduces genetic gain of the major traits (100). If no change is wanted for a specific trait, its desired gains can be set at zero, or if it has no economic value it can be excluded from the index (77,88).

Rosielle and Frey (77) criticized DGI for its use of minor traits in which improvement is not important. Their interpretation of DGI being, a modification of the restriction selection index in which the ratio of improvement for all traits is fixed. Their index does not use minor traits for which improvement is not important, to assist in selection. However, Tai (89) proposed a desired gain index in which the secondary traits can be used to assist selection for those traits having specified gains in the index selection.

The selection for quantitative traits when using DGI is complicated by qualitative characters such as monogenically inherited disease resistance. If a long term recurrent selection program for quantitative traits was adopted, it would probably be advantageous to select first quantitative traits under disease free conditions and subsequently introduce resistant genes by backcrossing (73). One of the major criticisms of DGI is that all desired gain values are reached in the same selection cycle. So the overall number of selection cycles needed for improvement of all traits is dependent on the trait in which improvement is slowest. This can be partially overcome by calculating several sets of index coefficients corresponding to different sets of desired gains, and comparing the gain to be expected by the use of each index (73).

There are several indices which are weight free or parameter free, one such index is the Elston weight free index (EWFI) which is considered to be a nonlinear index (20). The EWFI, or log of it, is designed to be independent of the relative importance of the traits used to construct it (85). The index value is the product of phenotypic deviations of each trait used in the index. This index is considered weight free because the measures are adjusted so that where each $X_i - K_i$, when $K_i \neq 0$,¹ adjusts each scale so that it "starts" at zero (20). This selection method is adequate for selecting a small number of individuals on the basis of several traits which are equally emphasized. If it is necessary for all individuals to be ranked this is not the correct index to use (20).

Rank summation index (RSI) is another parameter free (variance and covariance estimate) index. The RSI was first described by Mulamba and Mock (69), when they reported successful improvement of density tolerance in the ETO Blanco maize population. In experiments done by Mock and McNeil (66) and Mock and Skrdla (67) using RSI, they found an adequate amount of genetic variability for cold tolerance in some 34 inbreds and 144 plant introductions that are adapted to the North Central region. Mulamba and Mock (69) suggest that RSI would be useful for preliminary studies of hybrids that may be carried on for further testing.

¹ X_i = mean value for the i th trait, K_i is the minimum or maximum acceptable value for the i th trait.

If selection weights were desired they could be used in RSI by weighting the rank for each trait for its relative importance. A decrease in the range and variance for each trait is usually associated with the change to ranks. Smith et al. (85) pointed out that by changing from actual phenotypic values to ranks is a non-linear transformation of the data, which would maintain the relative rankings of the value for each trait. He also stated, that the RSI is most efficient when heritabilities are high, equal or nearly equal and the correlations among traits are either favorable or small.

Crosbie et al. (7), measured an improvement in cold tolerance traits in two maize populations using the EWF and RSI. These indices were suggested by the researchers for improvement of a composite of traits, where there seems to be no logical economic weights. Also, these indices can be used by the breeder when estimates of heritabilities and correlations among traits are not available (7).

These indices should also be considered when large differences in variances of index traits, are found across populations (7). Crosbie et al. (7), also found the EWF and RSI combined: 1) simplicity of use, 2) freedom from the need to estimate genetic parameters, and 3) good selection differentials and predicted gains in each trait and 4) a good aggregate genotypic value across

cycles. Elston weight free index and RSI were also shown to be dependable across selection cycles and tended to give small ranges in size of predicted gains across cycles (7).

Cold Tolerance

Early planting of maize in the U.S. corn belt region has been shown by Pendleton (70) to be advantageous for various reasons; 1) shorter plants with lower ears and better standability, 2) dryer grain for earlier harvest, 3) pollination before hot, dry days of late summer, 4) pollination and grain filling during long light days, and 5) reduction in soil water evaporation because of early shading. In a later experiment conducted by Pendleton and Egli (71), it was reported that early planted maize which flowered before later planted maize was more efficient in terms of grain produced per unit leaf area. It also has been demonstrated in several experiments, that early planted maize would out yield later planted maize (5,11).

Cold tolerance in maize can be defined by: the ability of a genotype to emerge from the soil and to grow vigorously after emergence in cold soil and air temperatures (13). The interest in cold tolerance in maize is not only for early planting as a method of increasing yields, but with use in the no-till and minimum tillage practices. These practices tend to lower early season soil

temperatures (65). In cool soils there is usually a delay in seed germination, emergence and early growth. In these soils, maize kernels are more prone to attack by soil pathogens. However, the use of seed treatment fungicides such as captan, thiram and carboxin, effectively solves the problem of decreased percent emergence due to soil pathogens (25,56,57,64).

Cold tolerance in maize has been evaluated by many experimenters in terms of percent emergence, emergence index (i.e. rate of emergence), and seedling dry weight (7,62,63,64,66,67,88). Mock and Eberhart (64) evaluated two U.S. corn belt maize populations (BSSS2 and BSSS13) using the three cold tolerance traits, both in the growth chamber and the field. They found that predicted selection response indicated that field selection for cold tolerance would be most efficient. Their results also indicated that improvements of cold tolerance traits by recurrent selection should be successful. Mock and Bakri (63) reported that more progress for cold tolerance could be made by recurrent selection in BSSS13 than in BSSS2 in field selection. While percent emergence and seedling dry weight were increased in BSSS13 population, emergence index was not changed. According to Mock and Bakri (63) there were too many inconsistent results in the BSSS2 population to come to any substantial conclusions about that population for cold tolerance characteristics. McConnell and Gardner (56) tested two adapted populations (SSCG and CTGG) and found that both populations

could be improved for cold tolerance traits by recurrent selections. However, in contrast to the findings of Mock and Eberhart (64), they felt field selection was less efficient than growth chamber studies, because the right field environment for cold tolerance studies is found in only one year out of four or five.

Hardacre and Eagles (27) used a different approach to evaluate cold tolerance in maize. They sought to determine at which temperature corn ceases growing heterotrophically and starts growing autotrophically. Six populations of maize from high altitude sources were crossed onto two U.S. corn belt dent inbreds and growth measured at 13°C. Their results showed definite differences in the ability to grow autotrophically in the crosses, but the U.S. hybrids (A632 X A659, A619 X A632, and W153R X A632) were not able to grow autotrophically at this temperature. Heterotrophic growth of all plants occurred at 13°C. It has been reported that growth by utilization of seed reserves, can occur at temperatures as low as 10°C (1,12,15,16).

McWilliam and Naylor (58) reported that photosynthesis in maize occurs slowly or not at all below 15°C in North American and European cultivars. Early seedling growth in maize is wholly dependent on seed reserves until the three to four visible leaf stage (6). At this stage the seedling then enters a transition

phase where growth may stop briefly if kept at 20°C, or stop for periods longer than 25 days at 13°C. Following this period between 35-55 days after planting at 13°C, the rate of photosynthesis either becomes enough to sustain autotrophic growth or the plant declines and dies (27).

Genetics of Cold Tolerance

As in any breeding program, improvement for traits such as cold tolerance is dependent upon the existence of genetic variability for that trait. The best breeding method to use in a program will depend on the relative magnitude of the additive, dominance, epistatic and maternal components of genetic variance and upon the magnitude of heritabilities and genetic correlations (87).

Genetic variation has been reported for cold tolerance traits in several U.S. corn belt dent varieties of maize, such as; BSSS2 and BSSS13 populations, (7,63,64), 34 adapted inbreds, (66) and in 144 plant introductions (PI's) adapted to each of the countries or ecological zones represented in the maize germplasm collection at the Plant Introduction Station at Ames, Iowa (67). Eagles and Hardacre (16) found genetic variation for time to emergence at 10°C in the population CIMMYT Pool 5. Eagles and Brookings (13) evaluated several populations for more rapid

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emergence than found in corn belt dents. They reported that all populations with germplasm from a highland Mexican origin germinated faster than corn belt dents, with the fastest containing a high proportion of germplasm from the Conico race. Mock and Eberhart (64) reported large genotypic variances for percent emergence (PCN and emergence index (EI) among S_1 lines from the two populations BSSS13 and BSSS2. In a subsequent study conducted by Mock and Bakri (63), they found, by use of index selection, a positive response for PCNTE and seedling dry weight (SEEDDW) but not EI.

Mock and Skrdla (67) reported large variances and heritabilities for cold tolerance traits in the 144 PI's they evaluated. They also reported large genotypic correlations for the three cold tolerance traits. Similar results were reported by Mock and McNeil (66) when testing 34 maize inbred lines adapted to the U.S. and Canada (these variances and heritabilities estimates were not biased by genotype X environment interaction). Mock (62) reported significant differences for inbred X year interaction in 34 adapted inbred lines in Iowa. Therefore, he concluded that for precise evaluation of cold tolerance traits in similar maize genotypes they should be tested more than one year.

It has been reported by several researchers that significant maternal effects are associated with inheritance of cold tolerance (24,74). Ventura (95) reported that maternal effects were greater than the paternal effects in cold tolerance, possibly due to the fact two genomes are contributed by the maternal parent to the endosperm tissue. Grogan (24) stated that maternal effects probably were more important for PCNTE and EI than for SEEDDW. However, McConnell and Gardner (57) studied reciprocal crosses of F_2 hybrids and concluded that maternal effects were not important for PCNTE and seedling vigor. Pesev (74) stated that the genetic mechanism of inheritance is rather complex and that better germination by single crosses between inbreds is due to complementary gene action in the seed embryo.

McConnell and Gardner (57) used generation mean analysis to show that most genetic variability for PCNTE and EI in 15 maize crosses was non-additive. They evaluated six inbreds and classified them warm (W) or cold (C). Their analysis indicated that epistatic gene effects along with additive and dominant gene effects contributed significantly to variation observed in emergence. Seedling vigor in this population was conditioned by additive and dominant gene effects. They also showed that C X C crosses were no better for cold tolerance than W X W or W X C crosses. The C X C crosses were slightly better for early season vigor, but percent germination and field emergence tended to be better in W X W and W

X C crosses. However, Grogan's (24) review of several studies, suggested that cold tolerance traits were controlled primarily by additive, multiple gene systems.

Disease Resistance

Disease organisms account for major worldwide losses in yield of maize. In the Northern Corn belt region some common disease causing organisms are; Exserohilum turcicum, Corynebacterium nebraskense, and Diplodia maydis.

Northern Corn Leaf Blight (NCLB), Exserohilum turcicum (Leonard & Suggs) (imperfect state of Setophoeria turcica Lutkell, Leonard and Suggs) was reported in Connecticut in 1889. Major damage occurred in maize in the early 1940's as susceptible hybrids replaced open pollinated varieties (18). Losses of as much as 50 percent of grain yield have been reported in severe epiphytotics. NCLB is also known to stress plants and predispose them to other diseases such as stalk rots (93).

E. turcicum overwinters in infected plant material, often forming chlamydospores within conidia. Conidia can be air borne and requires available moisture for germination. This fungus invades xylem vessels by leaf penetration and grows into infected xylem vessels over a several day period. It then colonizes the adjacent leaf chlorenchyma and parenchyma tissue. The invaded leaf tissue then may wilt rapidly and necrotic lesions can form (33).

There are two types of plant resistance to E. turcicum found in various germplasms of maize. Commercial hybrids may have either polygenic, monogenic (Ht gene), or a combination of the two types of resistance (23,31,32,34,35,38,42,50,51,75). Resistance, which is quantitatively inherited, affects the development of epidemics by reducing the number and the size of lesions formed (75). Quantitatively, it ranges from high resistance (few lesions formed) to low resistance (many large sporulating lesions formed) (18,41). Jenkins and Robert (42) reported that resistance was partially dominant and controlled by several genes, some of which showed major effects. Jenkins et al. (44) reported that because of the additive gene action found in maize, it was possible to improve populations for resistance by means of recurrent selection. Hooker (33,39) found that by incorporating Ht genes into inbred lines already possessing polygenic resistance, it was possible to increase the degree of resistance as defined by a change in lesion number or lesion type. In other experiments, low correlations between resistant lines and their progeny were reported, so it was concluded that there must be some non-additive type of gene action occurring (41,43).

There are several dominant Ht genes available for monogenic resistance, but only one gene (Ht₁) is presently used to any extent in commercial hybrids (31,40,75). Monogenic resistance, as determined by these Ht genes, is characterized by the formation of

reduced chlorotic lesions and delayed necrosis. Only sparse hyphal growth occurs and only a few spores are produced on lesions. The secondary spread of the pathogen is also impeded (33,75). Although resistance is inherited as a single dominant gene, varying degrees of chlorotic lesions and necrosis were observed when genes from different sources for resistance necrosis, while other plants were used.

Even though a backcross breeding method is used to put the (Ht) resistant gene into inbred lines, it has been shown by several experimenters that a quantitative type of resistance is effective in recurrent selection programs (34,41,44,61).

Goss' Wilt or Leaf Freckles and Wilt of maize is caused by the bacterium Corynebacterium nebraskense (2). It was first observed on two farms in South-central Nebraska in 1969 (79). Since then, it has spread throughout that state and into the bordering states of Colorado, Kansas, Iowa, and South Dakota (47), and more recently in areas of Illinois, Wisconsin and Minnesota (98). Goss' Wilt has been reported to reduce grain yield of maize by as much as 50 percent (4). Researchers looking for resistance to this bacteria have found several sources of varying degrees of resistance within the existing maize germplasm.

The characteristic symptoms of Goss' Wilt are dark green to black water soaked spots along the margin of developing leaf lesion. Bacterial exudate droplets may appear on the surface of the leaf as lesions enlarge. A crystalline substance, which shines in sunlight, may appear as the droplet dries (98). The maize plant can be infected at any age; seedlings may die sooner than older infected plants. Older plants may not produce tassels and ears depending on age at infection (79). Systemically infected plants may have discolored vascular bundles. The pathogen has been found in most parts of the maize plant, including roots, stems, leaf blades and sheaths, tassels, husks, silks, cobs and kernels (4,80,98).

The most common source of infection comes from overwintering bacterium in diseased corn residue (95,98). The bacteria can be seed borne on the outside of the seed coat or it may be carried internally (80). Once an infection is started it can spread to other plants by wind and rain. Injury to the maize plant increases the chance of plant infection; sandblasting, hail and turbulent weather associated with wind and rain will cause small abrasions that allow the disease organism to enter the plant (98).

Resistant hybrids are considered the best alternative for disease control (22). Other alternatives, such as deep plowing of infected maize stubble, are not very practical or economical in

reduced tillage and continuous corn production areas. Burning off corn stubble in the fall or spring to reduce disease potential has severe disadvantages. It can increase soil erosion by wind and rain and decrease moisture catching capacity of the soil (98).

In studying the genetic mechanism of disease resistance to Goss' Wilt, Gardner and Schuster (22) made crosses between maize varieties rated susceptible and tolerant to the pathogen. Crosses of susceptible x susceptible, susceptible x tolerant and tolerant x tolerant lines tend to be intermediate between respective parents. There may be more than one major gene locus controlling disease reaction. Martin et al. (54) reported the inheritance of susceptibility and resistance to be quantitative in nature.

Susceptibility to Goss' Wilt was found to be partially dominant from findings that F_1 readings of crosses between resistant and susceptible lines were generally greater than the midparent values (54). Therefore, breeding techniques which concentrate on additive gene effects (such as recurrent selection) should be effective in breeding for resistance to Goss' Wilt (54).

Diplodia stalk rot in maize, incited by the fungus Diplodia maydis, is found throughout the U.S. and several other countries of the world. Yield losses associated with Diplodia stalk rot are caused by light kernel weight and missed ears due to stalk lodging (9,92). Grain yield losses were estimated at 8.6 percent by Hooker

and Britton (36), due mainly to kernels that failed to develop fully because of stalk rots.

The disease organism overwinters as pycnidia on plant debris and as pycnidia or mycelium on the kernel. In warm, wet conditions, spores are extruded from pycnidia and disseminated by rain, wind and insects. Infection of the maize plant by the pathogen occurs during warm, moist weather through the corn mesocotyle and roots. The fungus does not invade the entire plant (9,92). The pathogen then grows into the plant and may cause the plant to die suddenly, giving it a grayish green color that resembles frost injury. The pith disintegrates, becomes discolored, and only vascular bundles remain intact (9,92).

Environment plays a major role in the development of stalk rot. Stress situations predispose plants to the stalk rot organism (9). According to Dodd (9) senescence of the pith tissue precedes stalk rot. Senescence begins at the top of the plant and progresses downward. Live pith tissue seems to resist the pathogen but dead tissue does not. Ullstrup (93) states that prior to invasion of the stalk by various fungi responsible for stalk rot, it is apparent that death of pith cells of the internode occurs along with cells in the nodal plates. Thus, a breeding program for superior hybrids may entail developing lines which reach physiological maturity before onset of stalk rot. This would mean full season

variety that would have dry kernels and green, solid stalks at harvest time. Some early work showed that removal of leaves increased susceptibility to stalk rot while removal of ears or prevention of fertilization increased resistance. Mortimore and Ward (68) reported that maize plant tissue which has high levels of soluble sugars in the pith at physiological maturity is more resistant to stalk rot. This is not to say that sugar content is directly responsible for resistance, but it is a indication of the physiological activity of the tissue.

Although mechanical strength of corn stalks is not directly associated with stalk rot resistance, mechanical strength along with stalk rot resistance is the objective of many breeding programs for good standability (8,53). Mechanical strength is important because when physiological maturity is reached, the parasites invade aging stalks, leaving mechanical strength as the remaining factor for standability. Martin and Russel (53) reported high correlations among stalk quality traits and proposed that simultaneous selection for stalk rot resistance and rind strength may be the best way to develop inbred lines with superior stalk quality.

Resistance to *Diplodia* stalk rot is believed to be conditioned by several loci and it appears to be governed by genes that are dominant or partially dominant to susceptibility (19). Miles

et al. (60) reported that in the two corn populations RSC and RSSSC, there was significant additive genetic variance for resistance to stalk rot. Russel (78) reported that the additive gene effects were of greater importance than non-additive effects for resistance in maize. Hooker (30) reported similar results in 25 inbred lines of maize. Kappelman and Thompson (48) studied the inheritance of resistance to Diplodia stalk rot in eight populations of maize. They found that additive gene effects were significant for all eight populations and dominance effects were significant for six. Sleper and Russel (82) reported stalk rot resistance and stalk strength were highly heritable and controlled by mostly additive gene action.

It has been demonstrated in several studies that increased resistance to Diplodia stalk rot can be accomplished by simple recurrent selection (44,46,53,60,61). Similar results were reported by Miles et al. (60) in the population RSC and RSSSC. Martin and Russel (53) reported lowering Diplodia stalk rot ratings from 3.5 to 1.8 with 3 cycles of S_1 recurrent selection in the synthetic BSl.

MATERIALS AND METHODS

The following experiments were designed to test the relative efficiency of two different selection methods used for simultaneous trait improvement. The selection index, originally proposed by Smith (83), was one of the methods evaluated by using three different modified selection indices. These three modified indices were: 1) desired gain index (DGI), (72); 2) Elston-weight-free index (EWFI), (20); and 3) rank summation index (RSI), (69). These three indices were compared against each other and against a second selection method known as independent culling levels (ICL), (28).

One hundred and twenty-five random S_1 lines used in the four experiments in this study were produced in a population selected for its early silking characteristic (SDS). The SDS population is comprised of 33 inbred lines and 24 single, three-way and double-cross hybrids adapted to the Northern region. The four experiments consisted of: 1) cold tolerance characteristics, 2) resistance to Exserohilum turcicum (Northern corn leaf blight), 3) resistance to Corynebacterium nebraskense (Goss' Wilt), and 4) resistance to Diplodia maydis stalk rot.

The cold tolerance experiment was planted on the SDSU Agronomy Farm in Brookings, on April 23, 1982. Twenty kernels from each S_1 line were hand-planted in two row plots, ten kernels per

row, 3.048 meters long with 1.016 meter row spacing. All kernels were pretreated with captan fungicide (25,37). A randomized complete block design with three replications was used. Three criteria were used to evaluate S_1 's for cold tolerance: 1) emergence index (EI), 2) percent emergence (PCME), and 3) seedling dry weight (SEEDDW).

The number of seedlings emerged from the soil was recorded on alternate days (beginning 18 days and ending 30 days after planting). From these data an emergence index was calculated using the formula proposed by Smith and Millet (86):

$$EI = \frac{\sum (\text{no. of plants emerged on a day}) (\text{days after planting})}{\text{total no. plants emerged 30 days after planting}}$$

The emergence index is an estimate of the rate of emergence. The S_1 's were also evaluated for percent emergence 30 days after planting. Seedling dry weights were obtained 45 days after planting by: a) cutting the seedlings at soil level, b) bagging on a row basis, c) forced air drying and d) recording of dry weights and dividing by number of plants harvested.

For the next three experiments, the 125 S_1 lines were screened for resistance to Northern Corn Leaf Blight (NCLB), Goss' Wilt, and Diplodia stalk rot. The S_1 lines were hand-planted, 30 kernels in a 9.15 meter row with 1.016 meters row spacing in a randomized complete block design, replicated three times. Each row of plants was divided into three groups of seven plants per group, to be inoculated with one of the three different organisms.

The first seven plants were artificially inoculated with E. turcicum by placing ground infected leaf material¹ into the whorl of seedlings at the four to five leaf stage (29,76). The same seven plants were then reinoculated two weeks later. Percent disease was recorded three times at ten day intervals, on a zero to five scale, starting approximately two weeks after 50% silking (33). The disease ratings that showed the greatest amount of variability between S_1 means were used in the construction of the various selection indices.

The rating scale used for NCIB, as described by Elliott and Jenkins (18), ranges from zero to five:

- 0 = no infection;
- 0.5 = very slight infection, one or two restricted lesions on lower leaves;
- 1 = slight infection, a few scattered lesions on lower leaves;
- 2 = light infection, moderate number of lesions on lower leaves;
- 3 = moderate infection, abundant lesions on lower and few on middle leaves;
- 4 = heavy infection, abundant lesions on lower and middle leaves extending to upper leaves;
- 5 = very heavy infection, lesions abundant on all leaves, plants may be prematurely killed.

Plants 8 thru 14 in each row were inoculated and rated for resistance to C. nebraskense. Isolates of C. nebraskense were maintained on nutrient broth-yeast extract (NBY) agar slants at 4°C. Inoculum was prepared from a mixture of five isolates

¹Collected from diseased plants in the 1981 nursery and ground in a Wiley mill with a 2mm screen.

streaked from stock cultures onto NBY media (4). The cultures were grown for 48 hours at 25°C before the bacterial cells were washed from the plates with distilled water. The cell suspension was diluted with distilled water to the desired optical density. A 0.5 absorbence reading was required to indicate a cell suspension containing 5×10^8 cells/ml (2,4).¹

The third seven plants, in the 4-5 leaf stage, were inoculated in all replications about two weeks after emergence. The pin-prick method described by Calub et al. (3) was used for artificially inoculating Goss' Wilt. Inoculations were made into the leaf whorl approximately three centimeters above ground level (4) and continued twice more into the leaf blades.

Each plant was rated three times, at one week intervals, starting ten days from inoculation date. The plants were evaluated as described by Calub et al. (3):

- 0 = no visible infection;
- 1 = slight infection (one to three pale spots on the leaf);
- 2 = moderate infection (four to ten pale spots and starting to spread);
- 3 = severe infection (11 or more pale spots with two or more spots often coalescing to form blight symptom or leaf starting to wilt);
- 4 = dead (whole leaf completely wilted or dried).

The disease rating period which showed the greatest variability between S_1 means was used in subsequent calculations of the various selection indicies.

¹Bausch and Lomb Spectronic 20 set at 420 nm was used.

The remaining seven plants in the plots were artificially inoculated with Diplodia maydis approximately two weeks after silking (60). The inoculum was maintained on potato dextrose agar (PDA) slants and was increased by transferring to PDA in petri dishes, three weeks before use. A spore suspension (2×10^5 spores/ml) was injected into the first elongated internode (60), above the brace roots.¹ Four weeks after inoculation the plants were cut off above the inoculated internode and the stalks were split longitudinally. Stalks were rated on percent area infected, using a scale described by Miles et al. (60), with the modification of adding group six to the scale. The scale used is as follows:

- 0 = no visible fungus
- 1 = 0 to 25% of the inoculated internode infected;
- 2 = 25 to 50% of the inoculated internode infected;
- 3 = 50 to 75% of the inoculated internode infected;
- 4 = 75 to 100% of the inoculated internode infected;
- 5 = 100% of the inoculated internode infected plus adjacent internode discoloration;
- 6 = premature death.

The S_1 lines were also grown in a recombination isolation block in Brookings in 1982. The S_1 families were grown in separate 9.14 meter rows, with a row of a composite of all S_1 's interplanted between every two rows of the individual S_1 's (the composite was also used as border rows). Each S_1 row was detasseled before pollination to assure pollination by the composite rows. The 125 S_1 rows were harvested separately in the fall.

¹A 50cc Vaco pistol grip rubber plunger syringe equipped with a special stainless steel needle was used.

The data were analyzed by analysis of variance and analysis of covariance methods (Table 1.) and variance and covariance components were estimated. Genotypic and phenotypic variances and covariances (Tables 2 and 3) were calculated based on the restricted model where $\sigma_{S_1}^2 = \sigma_A^2$.¹ Estimates of genetic and phenotypic correlation coefficients (Table 4) and heritabilities (Table 2) were calculated for all combinations of traits or each trait, respectively, by using the appropriate linear combinations of the estimates of genetic and phenotypic variances and covariances.

The estimates of genetic variance and covariance were used in the DGI used for multi-character selection. The general formula for the selection index is defined as: $I = \sum_{i=1}^m b_i x_i$, where b_i = ith index coefficient, x_i = ith phenotypic value (7). The desired gain index (DGI) used the formula $b = V^{-1}g$, to calculate the vector of index coefficients (Table 5.). In this formula, V^{-1} is the inverse of the genetic variance-covariance matrix, (values from Tables 2 and 3) which is multiplied by g^* , (Table 5.) the vector of desired genetic gains. Thus, the resulting index is:

$$I = -106.41 \text{ (emergence index)} + 323.93 \text{ (percent emergence)} \\ + 521.89 \text{ (seedling dry weight)} + 14.60 \text{ (Goss' Wilt rating score)} \\ + -6.39 \text{ (NCLB rating score)} + -.71 \text{ (stalk rot rating score)}.$$

¹ $\sigma_{S_1}^2$ = variance of S_1 lines; σ_A^2 = additive genetic variance.

Table 1. Form of single year analysis of variance and covariance for S_1 line means, with r replications and t S_1 lines.

Source of variation	Degrees of freedom	Expected mean square or mean cross products
Total	$tr-1$	
Replicates	$r-1$	$\sigma_E^2 + t\sigma_r^2$
Treatments (S_1)	$t-1$	$\sigma_E^2 + r\sigma_{S_1}^2 *$
Error	$(r-1)(t-1)$	σ_E^2

* $\sigma_{S_1}^2 = \sigma_A^2$, if $\sigma_D^2 = 0$, $\sigma_I^2 = 0$.

Table 2. Variance components and heritability estimates for cold tolerance traits and three disease scores from S_1 analysis.

Traits ^{ab}	Means	σ_P^2	σ_G^2	σ_E^2	h^2
EI	23.344	2.736	.088 [†]	2.647	.032
PCNTE	.842	.015	.002 ^{**}	.013	.133
SEEDDW	.470	.018	.006 ^{**}	.013	.310
Wilt	1.372	.219	.102 ^{**}	.117	.466
NCLB	2.577	.484	.364 ^{**}	.120	.752
STLKRT	2.487	1.167	.487 ^{**}	.680	.417

^a σ_P^2 = phenotypic variance; σ_G^2 = genotypic variance; σ_E^2 = environmental variance; h^2 = heritability.

^b EI = emergence index; PCNTE = percent emergence; SEEDDW = seedling dry weight; Wilt = Goss' Wilt; NCLB = Northern Corn Leaf Blight; STLKRT = Diplodia stalk rot.

[†] Significant at 0.26 level of probability.

^{**} Significant at 0.01 level of probability.

Table 3. Estimates of components of covariance.
 Genotypic covariance above diagonal, phenotypic covariance
 below diagonal.^a

	EI	PCNTE	SEEDDW	Wilt	NCLB	STLKRT
EI		.004	.009	.018	-.012	-.010
PCNTE	-.100		-.005	.002**	-.002**	-.008
SEEDDW	-.165	.007		-.001	-.002**	.003
Wilt	-.165	.006	.013		-.006	-.009**
NCLB	.101	.000	-.009	.125		-.003
STLKRT	.034	.007	-.016	-.009	.088	

** Significant at 0.01 level of probability.

^a EI = emergence index; PCNTE = percent emergence; SEEDDW = seedling dry weight; Wilt = Goss' Wilt; NCLB = Northern Corn Leaf Blight; STLKRT = Diplodia stalk rot.

Table 4. Estimates of genetic correlation for cold tolerance traits and disease ratings above diagonal, phenotypic correlation below diagonal.^a

	EI	PCNTE	SEEDDW	Wilt	NCLB	STLKRT
EI		.271**	.389**	.194*	-.068	-.046
PCNTE	-.500**		-.145	.145	-.072	-.251**
SEEDDW	-.745**	.420**		-.059	-.045	.058
Wilt	-.077	.104	.208**		-.167	-.039
NCLB	.076	-.001	-.010	.385**		-.008
STLKRT	.019	.053	-.111	-.018	.117	

^a EI = emergence index; PCNTE = percent emergence; SEEDDW = seedling dry weight; Wilt = Goss' Wilt; NCLB = Northern Corn Leaf Blight; STLKRT = Diplodia stalk rot.

*,** Significant at .05 and 0.01 level of probability, respectively.

Table 5. Values of desired genetic gains, and calculated estimates of index coefficients. ^a

	<u>Desired Genetic gains (g)</u>	<u>Index Coefficients (b)</u>
EI	-3.344 days	-106.41
PCNTE	9.0%	323.93
SEEDDW	.33 gms	521.89
Wilt	-.372 [†]	14.6
NCLB	-.577 ^{††}	-6.39
STLKRT	-.487 ^{†††}	-0.71

^a EI = emergence index; PCNTE = percent emergence; SEEDDW = seedling dry weight; Wilt = Goss' Wilt; NCLB = Northern Corn Leaf Blight; STLKRT = Diplodia stalk rot.

[†] Decrease in rating scale 0-4.

^{††} Decrease in rating scale 0-5.

^{†††} Decrease in rating scale 0-6.

Indicies of the 125 S_1 lines were ranked high to low and then equal amounts of seed from the topcrosses of the top 12 S_1 entries (ten percent selection pressure) were combined to form population A.

The Elston weight free index (EWFI) was calculated by $I = II_{i=1}^m (X_i - K_i)$, where X_i is the S_1 mean for each of the traits measured, K_i represents the highest or lowest acceptable boundary for each variable. If the K_i values were greater than 24.5, 3.0, 3.5, and 3.5 for EI, Goss' Wilt, NCLB and Diplodia stalk rot respectively, or the K_i values were less than .85 and .47 for PCNTE and SEEDDW respectively, then the value would equal zero and the entry dropped. From the resulting index, 24 acceptable entries were ranked high to low and equal amounts of seed from the topcrosses of the top 12 S_1 's were combined to form population B.

The third type of selection index compared in this study is the rank summation index (RSI), proposed by Mulamba and Mock (69). The S_1 families were ranked from highest to lowest value (PCNTE and SEEDDW were premultiplied by -1.0) for each of the six traits separately and the index calculated by summing the ranks of the six traits, $I = \sum_{i=1}^m \text{Rank } X_i$. Equal amounts of seed from the topcrosses of the top 12 S_1 lines with the greatest index values were combined to form population C.

The second selection method used was independent culling levels (ICL) (28). In this type of selection scheme, maximum or minimum levels for each trait are set (depending on whether a lower or higher value is desirable for each) and if an entry is above or below the desired level the entry is eliminated. Overall trait means were first used as culling levels but only seven of the needed 12 S_1 entries were retained. To increase the number of entries retained, culling levels were increased to 105% of the means for; EI, Goss' Wilt, NCLB and stalk rot, giving us values of 24.411, 1.438, 2.705, and 2.612, for the respective traits. Similarly, the independent culling levels for PCNTE and SEEDDW were lowered to 95% of the mean, resulting in independent culling levels of .80 and .447 respectively. At these culling levels we were able to obtain the 12 needed S_1 entries to construct population D.

The four synthesized populations (A,B,C,D) along with a representative sample of the original population (E) were planted in two separate experiments on the Agronomy Farm in Brookings in 1983 to determine realized gains for the four multiple trait selection schemes.

The cold tolerance experiment was hand-planted in 3.1 meter rows, consisting of ten kernels per row, spread 101.6 cm between row, in six row plots for each population. A randomized complete block design, replicated ten times was used. Due to the wet field

conditions in 1983, planting was delayed until May 5th. The five populations were measured for the same cold tolerance traits described previously.

The five populations were also planted in the 1983 disease nursery in Brookings. The populations were planted in two row plots 9.23 meters long and spaced .914 meters apart. A randomized complete block design with ten replications were used. The rows were overplanted and thinned to 36 plants per row.¹ The first 13 plants per row were inoculated with E. turcicum, the next 10 plants were inoculated for with C. nebraskense and the last 13 plants inoculated with D. maydis. The inoculation techniques and disease assessment scales were the same for each organism as the previous year.

Single trait means of the four selection schemes were compared to the means of the original populations as a measure of realized gain from selection for each trait. The relative efficiencies of the selection schemes were expressed by their: 1) selection differentials, 2) predicted gains and 3) aggregate genotypic values. Selection differentials for each trait were computed by subtracting the original population mean from the mean of the selections (10% selection intensity) and expressed as a percentage of the single-trait differentials. The predicted gain

¹Planted with a two row, John Deere Maxemerge planter.

for each trait was calculated by multiplying selection differentials by heritability estimates for their respective traits. The predicted gains for individual traits were also expressed as a percentage of gain predicted from single-trait selection (at 10% selection intensity). Finally, the aggregate genotypic value was the sum of the genetic gains of all traits.

RESULTS

The estimates of narrow sense heritability (h^2) showed large differences among all traits (Table 2). The h^2 estimate for NCLB (.75) was the largest value and EI (.03) was the smallest value of all traits. The estimate of genetic variability for EI was found to be significant at the .26 level of probability. Although this was relatively low, the trait was included in the study because this trait has been an important part of previous cold tolerance studies and should not be ignored.

When comparing the means of the six traits in the four resynthesized populations versus the original population, few significant ($p \geq .05$) differences were detected (Tables 6 and 7). The only significant differences among the populations were in the NCLB ratings taken at the first rating date in the RSI and EWFI.

There was a noticeable amount of variation in selection differentials between the four selection schemes for cold tolerance (Table 8). The DGI was the most efficient index in selection for EI and SEEDDW, with the ICL method only half as efficient as DGI for improvement of these traits. Rank summation index and EWFI were about equal in efficiencies in selection for EI and SEEDDW. The EWFI showed the greatest efficiency for selection of PCNTE, with DGI and ICL schemes being intermediate in efficiency for this

Table 6. Means of disease resistance ratings for each selection scheme and original population in the 1983 nursery.

Selection Schemes ^a					
Diseases ^b	DGI	EWFI	RSI	ICL	ORP
Wilt (rating 1)	1.75	1.74	1.73	1.71	1.79
Wilt (rating 2)	2.41	2.47	2.43	2.20	2.47
Wilt (rating 3)	2.54	2.58	2.52	2.46	2.57
NCLB (rating 1)	2.42	2.21*	2.15*	2.35	2.57
NCLB (rating 2)	2.58	2.48	2.44	2.49	2.70
NCLB (rating 3)	2.69	2.68	2.75	2.69	2.86
STLKRT	4.25	4.09	4.09	4.06	4.10

^a DGI = desired gain index; EWFI = Elston weight free index;
RSI = rank summation index; ICL = independent culling level;
ORP = original population.

^b Wilt = Goss' Wilt, ratings on a scale of 0-4.
NCLB = Northern Corn Leaf Blight, ratings on a scale of 0-5.
STLKRT = Diplodia stalk rot, ratings on a scale of 0-6.

* Significantly different from original population at .05 level of probability.

Table 7. Means of cold tolerance traits for each selection scheme and original population in the 1983 nursery.

Selection Schemes^a

Traits ^b	DGI	EWFI	RSI	ICL	ORP
EI	21.41	21.10	21.34	21.48	21.28
PCNTE	.72	.76	.72	.70	.72
SEEDDW	1.04	1.11	1.11	1.02	1.06

^a DGI = desired gain index; EWFI = Elston weight free index;
RSI = rank summation index; ICL = independent culling level;
ORP = original population.

^b EI = emergence index; PCNTE = percent emergence; SEEDDW = seedling dry weight.

No significant difference found at the .01 or .05 levels of probability.

Table 8. Selection differentials (at 10% selection intensity for single traits and selection indicies) for cold tolerance and disease resistance for different selection indicies expressed as a percentage of the single-trait selection differential.

Selection scheme ^a	Traits ^b					
	EI	PCNTE	SEEDDW	Wilt	NCLB	STLKRT
DGI	92.6	62.5	70.0	-8.5 [†]	15.7	-16.3 [†]
EWFI	59.0	75.0	56.7	1.5	28.5	14.3
RSI	66.7	37.5	53.3	38.1	43.8	25.3
ICL	37.0	50.0	30.0	38.5	40.0	30.0

^a DGI = desired gain index; EWFI = Elston weight free index;
RSI = rank summation index; ICL = independent culling level.

^b EI = emergence index; PCNTE = percent emergence; SEEDDW = seedling dry weight; Wilt = Goss' Wilt; NCLB = Northern Corn Leaf Blight; STLKRT = Diplodia stalk rot.

[†] Selection differential values are in a non-desireable direction.

trait. Rank summation index gave the lowest selection differential percentage value (38.9) for PCNTE.

The relative efficiencies of selection differentials for the three disease resistance ratings were shown to have large differences between all indices. The variation between indices for Goss' Wilt showed RSI and ICL with the largest differential value and EWFI gave a very low differential value (1.5%). The DGI value for Goss' Wilt had a negative (undesirable) selection differential (-8.5%). The selection differentials of RSI and ICL for resistance to NCLB and Diplodia stalk rot were the largest values obtained for all selection schemes. The EWFI was intermediate in efficiency for NCLB and Diplodia stalk rot resistance. Desired gain index was the least efficient of all the selection schemes for NCLB and stalk rot ratings, with stalk rot rating, like Goss' Wilt, having a negative (undesirable) selection differential of -16.3%.

Small genetic gains per cycle were predicted for all selection methods as compared to those reported by Crosbie et al. (7), and Miles et al. (60). Expected genetic gain is one-half of that expected had both parents been controlled at pollination time, to those of the respective selected S_1 's. However, because the male plants could not be selected before flowering, the S_1 rows that were selected at harvest time had been pollinated by pollen from the original population. Based on predicted gains, RSI and ICL

appear to be the best selection indices when all traits are considered. Predicted genetic gains for cold tolerance traits tended to be higher for DGI and EWFI but the more favorable values in the disease ratings for RSI and ICL offset its lower predicted gains for cold tolerance traits. The DGI produced positive (unfavorable) predicted genetic gains for Goss' Wilt and Diplodia stalk rot ratings (Table 9). However, DGI predicted the largest genetic gains for EI and SEEDDW of all selection schemes. The EWFI produced the largest predicted gain for PCNTE but all other values were intermediate for all traits except Goss' Wilt, which was much lower than predicted values for RSI or ICL schemes.

The relative index efficiencies, on a single trait basis for predicted gain (expressed as a percentage of the single trait selection) were the same as those calculated for selection differentials. This is to be expected since predicted gains are a function of selection differentials. So all respective observations made in the discussion for selection differentials on relative index efficiencies for each trait, will also apply for relative efficiencies of predicted gains.

For an overall comparison of each of the four selection schemes, the aggregate genetic gain of all six traits were compared (Table 10). We found RSI with the largest value of .366 and ICL at .351. The EWFI proved to be an average index with an aggregate genetic value of .208 and DGI least desirable with a .056 value.

Table 9. Predicted gains (per cycle) expressed in genetic deviation units, for cold tolerance traits and disease resistance for 125 S_1 families and relative index efficiencies.

Selection scheme ^a	<u>Predicted Gains</u>						<u>Relative Index Efficiencies</u>					
	<u>EI</u> ^b	<u>PCNTE</u>	<u>SEEDDW</u>	<u>Wilt</u>	<u>NCLB</u>	<u>STLKRT</u>	<u>EI</u>	<u>PCNTE</u>	<u>SEEDDW</u>	<u>Wilt</u>	<u>NCLB</u>	<u>STLKRT</u>
DGI	-.025	.005	.021	.014*	-.068	.049*	92.6	62.5	70.0	-8.3 [†]	15.7	-16.3 [†]
EWFI	-.016	.006	.017	-.003	-.123	-.043	59.3	75.0	56.7	1.5	28.5	14.3
RSI	-.018	.003	.016	-.064	-.189	-.076	66.7	37.5	53.3	38.1	43.8	25.3
ICL	-.01	.004	.009	-.065	-.173	-.090	37.0	50.0	30.0	38.5	40.0	30.0
STS	-.027	.008	.03	-.168	-.432	-.30	100	100	100	100	100	100

^a EI = emergence index; PCNTE = percent emergence; SEEDDW = seedling dry weight; Wilt = Goss' Wilt; NCLB = Northern Corn Leaf Blight; STLKRT = Diplodia stalk rot.

^b DGI = desired gain index; RSI = rank summation index; EWFI = Elston weight free index; ICL = independent culling levels; STS = single trait selection.

[†] Values in non-desirable direction.

Table 10. The aggregate genetic gains of the four selection schemes
(sum of genetic gains of all traits, for respective index).

Selection scheme ^a	Aggregate genetic gains
DGI	.056
EWFI	.208
RSI	.366
ICL	.351

^a DGI = desired gain index; EWFI = Elston weight free index;
RSI = rank summation index; ICL = independent culling level.

When comparing the original S_1 lines that were selected by each of the four methods, the DGI had six of the twelve S_1 lines in common with RSI, seven in common with EWFI, and three in common with ICL method. Rank summation index had seven S_1 lines in common with the EWFI and six with ICL method. The EWFI had five S_1 lines in common with the ICL method.

Estimates of genetic correlations (Table 4) showed EI to be significantly positively correlated with PCNTE, SEEDDW and Goss' Wilt. A negative correlation estimate was observed between PCNTE and stalk rot. Correlations between these traits, although statistically significant, were not large enough to alter our selection methods for correlated traits. No other significant genetic correlations were observed between cold tolerance traits and disease resistance ratings.

DISCUSSION

The heritability (h^2) values estimated in this study for cold tolerance traits were much lower than reported by other workers (62,66,67). The h^2 values were based on a single year data so the S_1 line estimates could have been biased upward by genotype by environment interaction, 1/4 of the dominance genetic variance, any epistatic genetic variance and possibly by maternal effects. The estimates of h^2 (Table 2) were .032, .146 and .31 for EI, PCNTE and SEEDDW respectively.

The assumptions used in the study to calculate narrow sense h^2 were that the S_1 variance ($\sigma_{S_1}^2$) equals the additive genetic variance (σ_A^2), and the dominance (σ_D^2) epistatic (σ_I^2) and genotype by environment interaction ($\sigma_{G \times E}^2$) variances equal zero (26). These assumptions may not be valid in this population due to the amount of non-additive gene action that has been cited as associated with these cold tolerance traits (24,64). It has been shown that there are large genotype by environment interactions associated with these traits (57).

Desired gains index and RSI have been found useful in improving cold tolerance traits in maize, but it has been suggested that selection should be based on more than one year's data (62,64). This is because of large genotype by environment interaction associated with these traits. The small amount of

genetic variability found among our S_1 lines for cold tolerance, showed that there was not enough genetic variability in this population for any measurable improvement in a single selection cycle with the present selection schemes.

The low amount of genetic variability detected for cold tolerance traits may be attributed to several factors: 1) the frequency of alleles for the cold tolerance traits, especially EI, may have been very low; or 2) the environment was not favorable for distinguishing among S_1 genotypes. Soil temperatures at time of planting in 1982 and 1983 were low, (Tables 11 and 12) but were taken in a low lying area with sod as ground cover. The soil temperatures usually are lower when the soil is covered with plant material in the Spring (65). During the 1983 cold tolerance experiment, several temperature probes were placed in the experimental field. Temperature readings were taken at the 5, 10 and 20 cm. levels in mid-afternoon 2 or 3 times a week. The temperature differences recorded in the field were up to 10°C higher than those recorded in nearby sod (table 12). Soil temperatures in the experimental plot may have been high enough to prevent cold stress upon the germinating seed (1).

The biases and assumptions that were discussed for cold tolerance heritability estimates also apply to heritability estimates for NCLB, Diplodia stalk rot and Goss' Wilt. Other

Table 11. Five day averages of soil temperatures taken on Agronomy farm in Brookings.
 With a 0% slope, sod ground cover and soil type of black silty loam.
 (Readings in celsius units)

1982										
Depth (cm)	Time	April 23-27	April-May 28-2	May 3-7	May 8-12	May 13-17	May 18-22	May 23-27	May-June 28-1	June 2-6
5	08	4.8	6.1	9.7	10.0	12.0	10.2	11.4	10.7	10.3
5	17	10.7	11.4	13.8	14.7	15.2	14.7	14.9	15.9	17.4
10	08	4.8	6.2	9.9	10.0	11.4	10.9	11.1	11.0	10.9
10	17	8.1	9.1	11.7	12.7	13.4	13.2	13.2	14.3	14.1
20	08	5.2	6.3	9.7	9.9	10.9	11.1	11.0	11.4	12.2
20	17	6.2	7.3	10.3	10.8	11.6	11.6	11.6	12.3	11.7
50	08	3.8	5.3	7.7	8.3	9.7	9.8	9.6	10.5	10.4
100	08	2.3	3.7	5.0	6.1	7.3	7.6	7.8	8.4	8.3

Table 12. Five day averages of soil temperatures taken on Agronomy farm in Brookings.
 With a 0% slope, sod ground cover and soil type of black silty loam.
 (Readings in celsius units)

1983										
Depth (cm)	Time	May 5-9	May 10-14	May 15-19	May 20-24	May 25-29	May-June 30-3	June 4-8	June 9-13	June 14-18
5	08	4.4	6.2	6.3	8.3	8.3	9.0	8.1	13.8	12.4
5	17	11.6	12.8	11.4	16.4	15.2	15.4	19.1	18.9	18.3
10	08	4.8	6.8	6.1	8.1	7.3	8.3	9.0	13.9	13.6
10	17	9.6	10.7	9.6	13.6	12.9	12.9	15.4	17.0	16.1
20	08	5.2	6.9	6.6	8.3	9.1	9.0	9.2	13.6	12.1
20	17	8.0	9.3	7.9	12.1	11.6	11.1	12.8	15.1	14.1
50	08	4.9	6.9	6.7	7.9	8.4	9.2	10.2	12.1	12.6
100	08	2.8	4.9	6.0	6.1	6.6	7.8	7.3	8.7	9.4

non-additive types of gene action have been reported in several maize populations for these three diseases (41,43,48,54). Genotype by environment interactions have also been found to be an important source of variation whenever studying the resistance to these disease organisms (4,9,41).

Our heritability estimate for NCLB resistance was larger in our population (.75) than was reported by Hughes and Hooker (41). Their results, along with several other researchers (34,42), showed additive genetic variance to be the most important part of the genetic variance for NCLB inheritance. We did observe a significant increase in disease resistance to NCLB with RSI and EWFI for the first rating date.

Diplodia stalk rot resistance was not significantly increased by any of the selection schemes, even though the heritability estimated was .417. It has been reported that stalk rot is a quantitatively controlled trait with mostly additive gene action and use of simple recurrent selection is a beneficial way of increasing disease resistance in maize populations (60,61). Jinahyon and Russell (45) reported a change in stalk rot rating from 3.7 to 1.7 by three cycles of S_1 selection in a Lancaster population. However, it is known that susceptibility to stalk rot is the result of a complex interaction between plants and environment (9,92). In the 1983 growing season, stalk rot was

severe in all populations. The mean rating of the original population was 2.5 in 1982 and 4.1 in 1983. There are a number of stresses which can increase stalk rot prevalence. Any stress which reduces carbohydrate production after silking will predispose plants to stalk rots (9,68,92).

Martin et al. (54) reported that selection methods which concentrate on additive gene effects should be useful in breeding for resistance to Goss' Wilt. In our selection schemes, no improvement was detected from selection for improved resistance to Goss' Wilt. As with many other traits in our experiments, predicted gain values among selection schemes were too small for a single selection cycle to make a detectable increase.

The use of selection differentials, predicted gains and aggregate genotypic values as reliable means of comparing selection indices, has been reported by several experimenters (7,14,49,88,99). The values of predicted gains for the three cold tolerance traits reported by Crosbie et al. (7) were much larger than predicted in this study. However, the predicted gains for NCLB and stalk rot ratings (on a single trait basis) were in agreement with those reported by Miles et al. (60).

When evaluating selection schemes by selection differentials, as a percent of single trait selection, we do not need to calculate relative index efficiencies of predicted gain. The

method used in calculating these two variables holds the respective ratios equal. This would benefit comparisons between selection schemes such as RSI, EWFI and ICL that do not need estimates of genetic parameters to assist in selection. These selection schemes can be compared for their relative efficiencies by their selection differentials.

The overall relative efficiency of the DGI was not as high as we would have expected. The DGI produced negative selection differentials for Goss' Wilt and stalk rot ratings and had the lowest aggregate genotype value. Similar results from DGI were reported by Crosbie et al. (7) when studying cold tolerance traits. They showed that the DGI was sensitive to the desired gain values used, whether set too large or too small for a given population. In our population the desired values may have been set too high for cold tolerance traits (Table 5) since our estimates of genetic variances were very low. This index may have been more efficient if several sets of desired gain values were used. Decreasing the desired gain levels for the cold tolerant traits may have resulted in larger realized gains for disease resistance. Therefore, an increase in disease resistance for Goss' Wilt and Diplodia stalk rot also may have been realized since heritability estimates were higher for disease resistance than for cold tolerance traits.

When considering aggregate genetic gains, RSI and ICL were the most efficient indices when selecting for cold tolerance and disease resistance in maize. The advantage of these selection schemes, as well as EWFI is that they are parameter free. It has been shown by other researchers that an inaccurate estimate of genetic parameter can seriously affect the accuracy of an index (97). The RSI is a more desirable type of selection scheme than ICL because all entries are listed in RSI where they are not in ICL. This is important if comparisons between entries are desired over years or locations. With the ICL method, a comparison of all entries is not possible. The RSI was also found to be simple to use and has been shown to be dependable over selection cycles (7,60).

The significant positive genetic correlations observed for EI with PCNTE and SEEDDW were unfavorable (Table 4). This indicates that selection for increasing PCNTE and SEEDDW would also increase days for EI. The phenotypic correlations for these traits were found to be significantly negatively correlated with EI. Therefore, selection based on the phenotypes for increase in cold tolerance for all three traits would not select the correct genotypes to improve EI. A significant positive correlation for EI with Goss' Wilt and a significant negative correlation for PCNTE with stalk rot were observed. These correlations have no biological explanation, and must be attributed to some other

unmeasurable factor present in this experiment or to random chance and possibly linkage disequilibriums.

Gain from selection may have been realized in all indicies for disease resistance if selection pressure for these traits had been increased. There was a large amount of genetic variation among S_1 lines for resistance to NCIB and this was the only trait improved by selection in the RSI and EWFI. Predicted gain for single trait selection was relatively large for Diplodia stalk rot so it should have been possible to increase resistance in the original population had enough selection pressure been applied. The original population seemed to be fairly resistant to Goss' Wilt so increasing resistance to this pathogen may not be as important as increasing resistance to the other pathogens. Since data were collected for only one year and one location the genotype by environment interaction may have greatly effected our estimate of genetic parameters and S_1 lines selected. By planting in more than one location, an estimate of genotype by environment interaction could be obtained; therefore, eliminating some of the biases in the selection indicies due to this source of variation.

The low amount of genetic variability found in this population for the three cold tolerance traits shows that gain from selection may be impractical in this case. These traits may have such a large genotype by environment interaction term that successful field studies are impossible in this population.

It has been suggested by McConnell and Gardner (56) that cold tolerance studies should be conducted in a growth chamber. Growth chamber studies may be useful in improving EI and PCNTE but may not be very effective in improving SEEDDW. Crosbie et al. (7) has suggested that total plot weights should be used for cold tolerance selection since it would be relatively easy to get observations over several locations.

In summarizing the relative efficiency of the four selection schemes, the RSI and ICL schemes were the most efficient for all three relative efficiency comparisons. The EWFI proved to be intermediate in efficiency when compared with the other selection schemes for all traits except for the significant improvement in NCLB resistance measured. The EWFI, like the ICL method, can be an undesirable index to use if all entries need to be listed in the index. The DGI proved to be the most inefficient index of all, because of the negative selection differentials and negative relative index efficiencies in predicted gains for Goss' Wilt and Diplodia stalk rot. It also was the lowest of all selection schemes for the aggregate genotypic value. They feel this would be a logical way to cope with the large genotype by environment interaction associated with these traits.

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